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Sex allocation, juvenile mortality and the costs imposed by offspring on parents and siblings

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competition;
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sex ratio;
sexual conflict;
sexual selection.

Abstract

Generally, sex-specific mortality is not expected to affect optimal patterns of sex allocation. Several authors have, however, made verbal arguments that this is not true if juvenile mortality is sex specific during the period of parental care. Here, we provide formal mathematical models exploring the effect of such mortality on optimal sex allocation. We confirm the prediction that biased production of the sex with higher mortality during care is favoured. Crucially, however, this is only true when juvenile mortality in the period of parental care frees up resources for their current/future siblings (i.e. the saved investment is transferable). Furthermore, we show that although optimal sex allocation is consistent with the theory of equal investment (as asserted by previous authors), thinking in terms of equal investment is not readily feasible in some scenarios. We also show that differences in early mortality overcome biased sex allocation such that the sex ratio at independence is generally, but not always, biased in the opposite direction from that at birth. Our models should prove useful to empiricists investigating the effect of sex-specific juvenile mortality and antagonistic sibling interactions on sex allocation.

Introduction

Sex allocation theory predicts the optimal division of resources into male and female reproductive function (West, 2009). Generally speaking, equal sex allocation is predicted (Düsing, 1884; Fisher, 1930). In dioecious species, this usually resolves to a primary sex ratio – the proportion of sons produced at fertilization – of 0.5 (i.e. equal numbers of sons and daughters produced). This occurs because the excess production of either sex reduces the mean reproductive output of individuals of that sex, lowering the returns offered by offspring of that sex from a parent's perspective (Düsing, 1884; Fisher, 1930). In this way, the primary sex ratio is under negative frequency-dependent selection. This prediction of equal investment can help us explain why so many species of animals produce sons and daughters in roughly equal numbers (assuming that the sexes are equally costly to produce in most cases; West, 2009).

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When sons and daughters are not equally costly to produce equal investment into each sex is still the optimal strategy, but this does not lead to a primary sex ratio of 0.5. For example, if sons cost three times as much as daughters to produce, equal investment would be a sex ratio of 0.25. The average reproductive output of sons would then be three times as much as that of daughters (because there are, on average, three females per male in the breeding population). In this way, natural selection leads to sex allocation that matches the value each sex offers their parents with the initial cost of producing that sex (Fisher, 1930).

The general prediction of equal investment into each sex is, in most cases, independent of sex-specific mortality (Leigh, 1970). Consider a species where the primary sex ratio is unbiased and costs of raising sons and daughters are equal, but males are twice as likely as females to die before reproducing. There will be, on average, twice as many females in the mating pool as there are males. Surviving males have double the average reproductive output of females, completely balancing out their elevated mortality. There is no selection for a sex ratio bias (Leigh, 1970). Exceptions occur, however, when mothers' condition predicts offspring

survival or mating success (and these therefore can break free from having to equal the average values for this sex, West, 2009), or when generational overlap allows periods of sex-specific mortality to be compensated for by biased sex allocation towards the rarer sex after unpredictable events (Werren & Charnov, 1978; Michler *et al.*, 2013), or in anticipation of such periods in predictable seasonal scenarios (Kahn *et al.*, 2013).

Another exception leading to a biased primary sex ratio exists when juvenile mortality occurs prior to independence in species with parental care (i.e. during the period of parental expenditure; Fisher, 1930). If parents pay a significant cost to raise offspring to independence, any young that die before that point could be seen as wasted investment. This waste takes a subtle form, however, if costs to parents accrue gradually during the parental care period. Parents obviously reap no fitness benefits through young that die, but not all investment is wasted if the death of an offspring frees the parent from paying all the care costs that would have accrued by the time the offspring reached independence. This saving can potentially be reallocated into other current or future offspring. In this case, sex differences in juvenile mortality lead to sex differences in both the mean expected cost of producing each sex and the expected returns. For example, if sons tend to die more often during the period of parental care, the average cost of sons will be greater for each son successfully reared to independence, but also less per son actually born (Fisher, 1930). The question then is, how should this affect optimal sex allocation?

Fisher (1930) briefly dealt with this scenario in his discussion of the theory of equal investment. With a particular focus on humans, he stated that if sons die more frequently during the period of parental care, they will be the 'cheaper sex' to produce, despite surviving to adulthood less often. He argued that natural selection would favour the situation where '... boys are the more numerous at birth, but become less numerous, owing to their higher death-rate before the end of the end of the period of parental expenditure'. (Fisher, 1930, p.143). As in the case of his enigmatic comments on 'runaway' sexual selection, Fisher's conclusion seems plausible, but the assumptions and calculations underlying his argument were not made explicit.

Since Fisher, this topic has received relatively little attention from theoreticians and empiricists alike (West, 2009). To our knowledge, no quantitative empirical test for an effect of sex-biased mortality during care on the primary (or indeed secondary) sex ratio has yet been attempted. This could be partly related to the difficulty of disentangling inherent differences in sex-specific mortality from compensatory responses by parents (e.g. providing more food to the 'weaker' sex).

Several mathematical models have dealt with sex allocation given sex-differential initial costs in species with discrete generations (e.g. Kolman, 1960; Charnov 1982). These models, however, assume that Fisher's assertion that the sex with greater mortality during the period of care is less costly is true. In particular, these models focus on the idea of a 'substitution cost' – if a mother foregoes an attempt to raise a son, how many daughters can she produce? The answer to this question is not immediately apparent for the case of differential juvenile survival. Consider, for example, the case where sons survive better than daughters during the period of parental care. Sons then impose a greater cost on their parents, but, at the same time, they are more likely to survive and provide their parents with grandoffspring. As is generally the case in sex ratio theory, we must also consider the effect of mate availability, which likewise is affected by offspring mortality. The situation is sufficiently complex that verbal arguments could mislead or, at least, gloss over hidden assumptions.

Here, we model optimal patterns of sex allocation, specifically taking into account sex differences in juvenile mortality, and the costs that offspring impose on their parents or siblings. In particular, we want to assess the validity of three widely made assertions: when sex-differential juvenile survival affects the relative costs of rearing sons and daughters, (i) parents should bias sex allocation towards the sex with greater mortality (Fisher, 1930), (ii) the optimal pattern of sex allocation is that which leads to equal investment (across the whole period of parental care) into the sexes ('The exact sex ratio favored is that which leads to the total investment in sons and daughters over the whole period being equal' – West, 2009 p. 20) and (iii) that the sex ratio at independence will be biased towards the sex with greater survival during the period of parental care – even though they were rarer at birth ('... sex ratio should be male biased early [assuming sons have higher mortality], but female biased near weaning' – Charnov, 1982 p. 29; see also West, 2009 p. 19).

Analytic matrix models

Below, we present the results from two analytic models of optimal sex allocation in relation to juvenile mortality. Model 1 ('maternal survival model') deals with the case where differential juvenile mortality affects the survival prospects of caring mothers. Model 2 ('sibling competition model') considers the case where differential juvenile mortality affects sibling survival (i.e. there is within-brood competition). We used a periodic two-sex matrix population modelling approach (Caswell, 2001). This involves breaking down a system into a series of distinct phases, then describing the transitions between successive phases (e.g. Jenouvrier *et al.*, 2010). At phase i, we have a population vector $\mathbf{P}_i$, which is the number of each type of individual at that particular time. Process i represents the transition from phase i to phase i+1 and is described by the projection matrix $\mathbf{A}_i$, such that $\mathbf{P}_{i+1} = \mathbf{A}_i\mathbf{P}_i$. Once these have been described, the equilib-

rium population dynamics can then be determined, and the reproductive values of different types of individuals calculated (see below; Brommer *et al.*, 2000; Pen & Weissing, 2000a). The advantage of this approach is that it allows us to describe complex systems incrementally in a series of conceptually simple steps.

Model 1: maternal survival model

First, we consider an iteroparous species that breeds once per year where mothers are responsible for sex allocation decisions and parental care. There are four separate phases and transitional processes to consider (Fig. 1): (i) population $\mathbf{P}_1$ consists of overwintering adult males (M) and females (F) who are ready to reproduce: $\mathbf{P}_1 = [M\ F]^{\mathrm{T}}$. The first process is sex allocation: females 'decide' whether they will produce a son or a daughter; one offspring is produced, and x denotes the probability of producing a son for any given reproductive event (i.e. the primary sex ratio). The first projection matrix is thus:

$$\mathbf{A}_1 = \begin{bmatrix} 0 & x \\ 1 & 0 \\ 0 & 1-x \end{bmatrix} \tag{1}$$

(ii) Now, the population $\mathbf{P}_2$ is made up of adult males as well as females who will go on to produce sons (F_S), or daughters (F_D): $\mathbf{P}_2 = [F_S\ M\ F_D]^{\mathrm{T}}$. Reproduction occurs next; parents each contribute half their genetic material to the offspring. Male reproductive success also depends on the per capita availability of mates (i.e. F/M):

$$\mathbf{A}_2 = \begin{bmatrix} 1 & 0 & 0 \\ 1/2 & F_S/(2M) & 0 \\ 0 & 1 & 0 \\ 0 & F_D/(2M) & 1/2 \\ 0 & 0 & 1 \end{bmatrix} \tag{2}$$

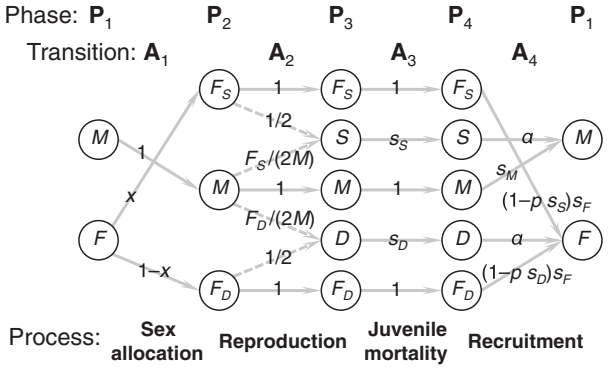

Fig. 1 Life cycle graphic for Model 1 (maternal survival). Solid grey lines indicate survival, whereas dashed lines are reproduction. The values on the lines indicate the probability that an individual from phase i survives/contributes genes to the corresponding class of individuals in phase i+1.

(iii) We then have adult males, sons (S), daughters (D) and females caring for either a son or a daughter: $\mathbf{P}_3 = [F_S\ S\ M\ D\ F_D]^{\mathrm{T}}$. Next, we deal with mortality during the period of parental care. Sons and daughters survive through this period with probabilities s_S and s_D, respectively, whereas mothers and fathers are assured survival. The projection matrix is thus:

$$\mathbf{A}_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & S_S & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & S_D & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \tag{3}$$

(iv) As before, we now have adult males, sons, daughters and females who have finished caring for either a son or a daughter: $\mathbf{P}_4 = [F_S\ S\ M\ D\ F_D]^{\mathrm{T}}$. The final process is overwinter survival (i.e. recruitment to next year's mating pool). Adult females and males overwinter with probabilities s_F and s_M, respectively. Adult female survival must, however, be reduced according to the costs associated with caring for the offspring the females recently produced. This cost is a negative function of how long the females had to care for their offspring, and the duration of care depends on the probability that the offspring survives. In this way, a female's own survival depends on her offspring's probability of survival (and hence its sex). We incorporate this cost in a simple, linear way: the survival of son-caring mothers is multiplied by $1 - p\ s_S$, whereas the survival of daughter-caring mothers is multiplied by $1 - p\ s_D$. Here, p ($0 \le p \le 1$) is a penalty paid by the mother. If $p = 0$, female survival is independent of the survival of their offspring. Thus, adult female survival through this period is either $(1 - p\ s_S)s_F$ for mothers who produced a son in the preceding phase or $(1 - p\ s_D)s_F$ for mothers who produced a daughter in the preceding phase. Both sons and daughters recruit to the adult population with probability α, which is not fixed but responds to population density. We thus use this parameter to introduce density-dependent survival at the juvenile stage only. Therefore, our final projection matrix is:

$$\mathbf{A}_4 = \begin{bmatrix} 0 & \alpha & S_M & 0 & 0 \\ (1-pS_S)_{S_F} & 0 & 0 & \alpha & (1-pS_D)_{S_F} \end{bmatrix} \tag{4}$$

We now want to set α such the population size is stable from 1 year to the next. We can do this by ensuring that the number of adult, breeding females at the start of 1 year is the same as the next. This is done by solving the following equation:

$$F = \alpha S_D (1-x) F + S_F (1-p S_S) x F + S_F (1-p S_D) (1-x) F \tag{5}$$

which gives us

$$\alpha = [1 - S_F (1-p S_S) x - S_F (1-p S_D) (1-x)]/[S_D (1-x)] \tag{6}$$

Here, if s_F or s_D are small, α could potentially be greater than 1. This makes no biological sense because juvenile survival from birth to recruitment ($\alpha\, s_S$ or $\alpha\, s_D$) would then exceed 1, which is impossible. If the persistence of a population requires impossibly high juvenile survival values, the population is in reality unstable and heading for extinction. Therefore, it is sensible to only consider cases where α remains below 1 (i.e. females and their daughters survive sufficiently often for the population to persist). That said, it is unlikely that optimal patterns of sex allocation, our main focus, change with population growth (or reduction) rates.

As above, we can find the stable number of males in the system:

$$M = (\alpha S_S x F)/(1 - S_M) \tag{7}$$

On average, $\alpha\, s_S\, x\, F$ sons and $\alpha\, s_D\, (1–x)\, F$ daughters survive to reach independence. We therefore know how the sex ratio at independence (y) is related to the optimal primary sex ratio:

$$y = (S_S x)/[S_S x + S_D (1 - x)] \tag{8}$$

The next step is to find the reproductive value at equilibrium of females who decide to produce either sons or daughters in phase 2 (i.e. immediately after making sex allocation decisions). Here, $\mathbf{P}_2 = \mathbf{A}\mathbf{P}_2$, where $\mathbf{A} = \mathbf{A}_1\mathbf{A}_4\mathbf{A}_3\mathbf{A}_2$. The dominant eigenvalue of this combined projection matrix $\mathbf{A}$ is thus a multiplicative factor of population size (Caswell, 2001), which is constrained to be one here (i.e. no population growth or reduction). The corresponding left eigenvector is then the reproductive values of the three types of individuals (F_S, F_D and M) in phase 2 (Brommer *et al.*, 2000; Pen & Weissing, 2000a). The optimal pattern of sex allocation (x) is that which balances the reproductive value of females that 'decide' to produce sons (F_S) with those that 'decide' to produce daughters (F_D). By setting the corresponding values of the left eigenvector to be equal, we can solve for optimal sex allocation:

$$x = \frac{1}{2} + \frac{1}{4}\frac{S_F p\,(S_D - S_S)}{1 - \frac{1}{2}S_F(1 - pS_D) - \frac{1}{2}S_F(1 - pS_S)} \tag{9}$$

This form makes it clear that the extent of primary sex ratio biases is proportional to the differential maternal survival cost imposed by sons or daughters (the numerator) relative to maternal life expectancy under the baseline assumption of no sex ratio bias (the inverse of the denominator).

Model 1: results

The optimal sex allocation depends on the survival of both sons and daughters during parental care, the survival of females (but not males) between years and the penalty imposed by surviving offspring on their mothers' survival while caring. Our model corroborates earlier verbal arguments that mothers should produce more of the sex with greater mortality during the period of parental care (Figs 2 and 3; Fisher, 1930; Charnov, 1982**)**. Furthermore, stronger sex allocation biases are predicted as sex-specific mortality differences increase (i.e. as the difference between s_D and s_S increases). As expected based on the null model for Fisherian negative frequency-dependent selection, equal sex allocation is favoured when there is no sex difference in offspring survival during the period of parental care.

Generally, the primary sex ratio is under strong negative frequency selection favouring equal allocation to sons and daughters. When maturing juveniles contribute relatively little to the total population in the following year, however, this selective pressure is weaker. There is thus more opportunity for mothers to produce biased broods without coming up against negative frequency-dependent selection (because biased primary sex ratios will have little effect on the sex ratio at independence). Consequently, our model predicts stronger sex allocation biases when maternal survival post-parental care is high (Fig. 2) and juvenile recruitment to next year's population size is low.

One important, and possibly underappreciated, point shown by our model is that biased sex allocation is only predicted if mothers obtain a 'saving' when a dependent offspring dies (analogous to the idea of a substitution cost; Charnov 1982). In other words, if a mother's survival (s_F) is completely independent of the fate of her offspring during the period of parental care (i.e. $p = 0$), then unbiased sex allocation is predicted. The more strongly maternal and offspring survival are causally linked (i.e. larger values of p), the greater the sex allocation biases predicted (Fig. 3).

The biases predicted by our model are generally modest (40–60% sons) depending on the above-mentioned parameters. This is mostly due to the limitations imposed by population growth (i.e. that $\alpha \leq 1$), which means we only consider a limited, but biologically relevant, parameter space (i.e. s_D and $s_S > 0.5$, $s_F > 0.7$ and $p < 0.3$, as in Figs 2 and 3). If offspring impose very large survival costs on their mothers (i.e. p close to 1), then too few females will survive to maintain the population, causing extinction. In some cases, adaptive sex allocation could worsen this effect. For example, if offspring impose a large cost on maternal survival and sons tend to die more during the period of care, a male-biased primary sex ratio is favoured. This will amplify any shortage of females in the population caused by the large cost imposed on mothers. It is also worth noting that slightly weaker sex allocation biases are predicted for higher offspring survival probabilities, given the same absolute survival difference between the sexes (compare with Model 2 below).

As an important conceptual aside, our model can easily be reformulated to incorporate a scenario where

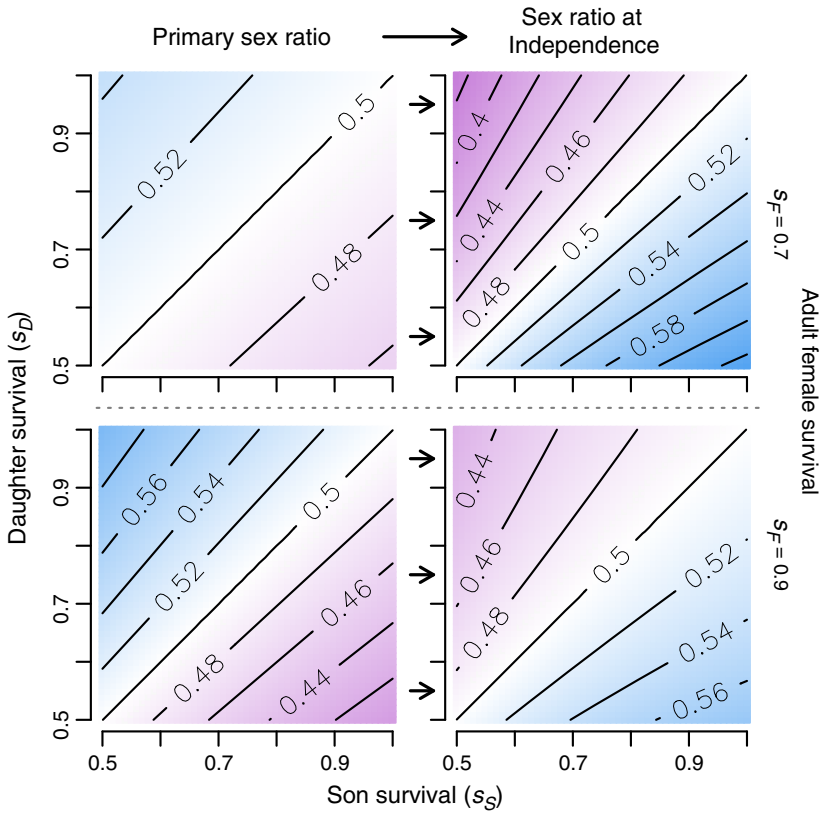

Fig. 2 Numerical examples of optimal sex allocation predictions from Model 1 (maternal survival) with respect to the survival probabilities of sons and daughters with two different levels of adult female survival. The panels on the left show optimal primary sex ratios (at fertilization), whereas those on the right show the resultant sex ratios at independence. Here, p = 0.2.

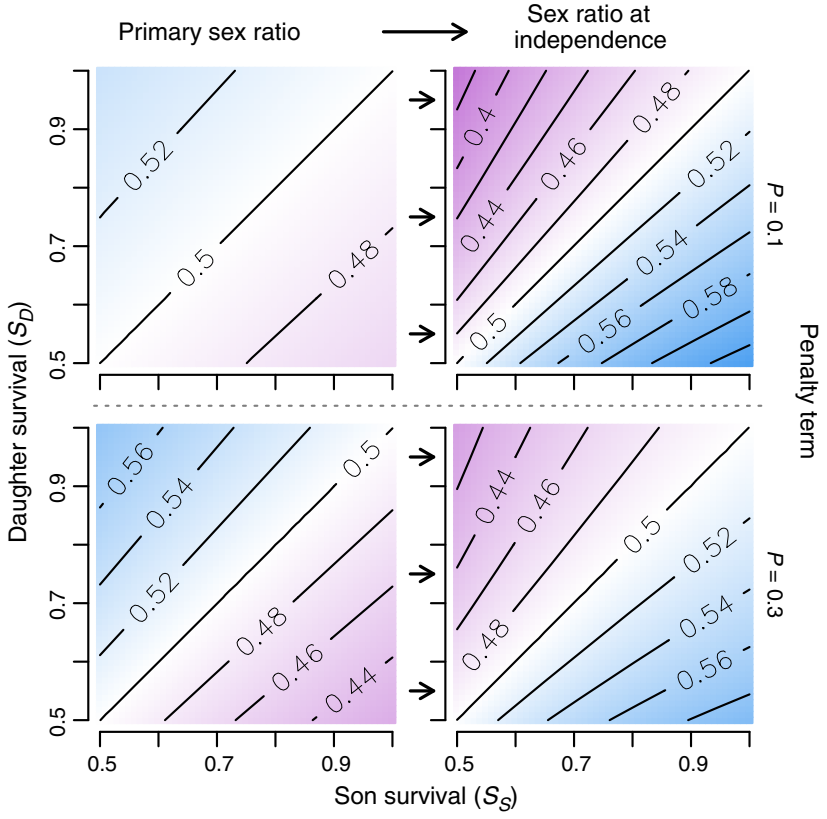

Fig. 3 Numerical examples of optimal sex allocation predictions from Model 1 (maternal survival), this time with two different levels of the penalty term p. Here, s_F = 0.8.

fathers provide parental care, whereas mothers still make the sex allocation decisions. Here, no matter how great the costs of care imposed on fathers, equal sex allocation is always favoured (see the supplementary information). This outcome re-emphasizes the importance of the role of a 'saving' in optimal sex allocation. Mothers are now afforded no saving from offspring that die before the end of parental care, so they have nothing to gain from biasing sex allocation (even though their mates would gain from it). This is also a clear example of sexual conflict over sex allocation decisions (this result was also derived in Pen & Weissing, 2000b). In the reformulated version, females do not pay a cost of providing care; thus, sex allocation is driven solely by negative frequency-dependent selection, and juvenile mortality follows the familiar results usually associated with adult mortality: it simply increases the per capita success of surviving offspring of the weaker sex.

Equal investment?

It is instructive to test whether the optimal pattern of sex allocation predicted by our model equates to equal investment, as predicted by several authors (e.g. West, 2009 p. 20). A female's investment for a given reproductive event is her sex allocation decision (x) multiplied by the potential cost of that decision (here, the probability that she dies before getting to reproduce again). Therefore, a mother's investment in sons is:

$$x\,[1-(1-p\,S_S)\,S_F] \tag{10}$$

Investment in daughters takes the form

$$(1-x)[1-(1-p\,S_D)S_F] \tag{11}$$

If we set these two investments to be equal and solve for optimal sex allocation, we find an identical solution to that obtained with the reproductive values approach (i.e. we rederive eq. 9). Therefore, equal investment into the sexes is indeed favoured, demonstrating that the scenario being modelled is a special case of the theory of equal investment as Fisher and others have asserted (Fisher, 1930 p. 143; West, 2009 p. 20).

Sex ratio at independence

When one sex suffers a higher rate of mortality during parental care, Model 1 shows that biased production of that sex can be favoured. However, in no cases did this bias persist to independence (Figs 2 and 3 right column). Whenever biased primary sex ratios were predicted, the sex ratio at independence was biased in the opposite direction. The effect of sex-specific mortality always outweighed any sex allocation biases.

Model 2: sibling competition model

We next consider a species where females always produce two young per brood and mothers are responsible for sex allocation decisions and parental care. During the period of care, offspring survival is dependent on the survival of their sibling (and hence influenced by their sex if mortality is sex-biased). Unlike Model 1, if an offspring dies, it does not affect its mother's survival, but instead its brood mate's (sibling's) survival can be improved. Note that this scenario, where the survival of mothers is independent of their offspring's fate, makes it quite hard to speak in terms of investment per offspring (as investment ought to be measured as a reduction in a mother's ability to produce more broods). The difficulty of applying equal investment logic makes this model a particularly interesting one for unravelling the adaptive dynamics of sex allocation decisions.

There are four separate phases and hence four transitional processes to consider in this system (Fig. 4): (i) The population $\mathbf{P}_1$ consists of overwintering adult males (M) and females (F) who are ready to reproduce: $\mathbf{P}_1 = [M\ F]^{\mathrm{T}}$. The first process is then sex allocation: females 'decide' whether they will produce two sons, two daughters, or one son and one daughter. The independent probability that a particular offspring is male (i.e. the primary sex ratio) is x. In this way, the probability that a female 'decides' to produce two sons is x^2 and so on. The first projection matrix is thus:

$$\mathbf{A}_1 = \begin{bmatrix} 1 & 0 \\ 0 & x^2 \\ 0 & 2x(1-x) \\ 0 & (1-x)^2 \end{bmatrix} \tag{12}$$

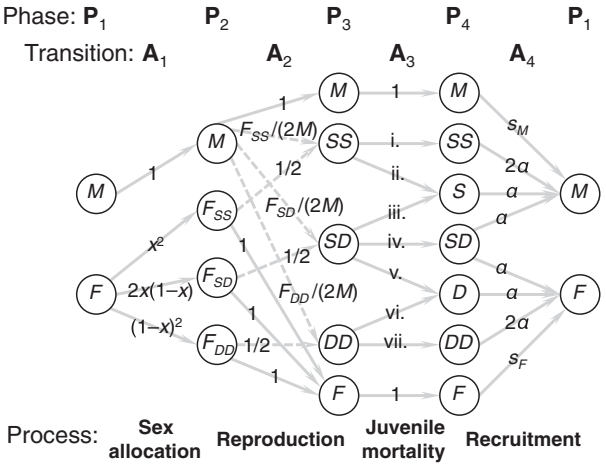

Fig. 4 Life cycle graphic for Model 2 (sibling competition). Solid grey lines indicate survival, whereas dashed lines indicate reproduction. The values on the lines indicate the probability that an individual from phase i survives/contributes genes to the corresponding class of individuals in phase $i + 1$. The values not shown are (i) $[(1-p\,s_S)\,s_S]^2$, (ii) $2(1-p\,s_S)\,s_S\,[1-(1-p\,s_S)\,s_S]$, (iii) $(1-p\,s_D)\,s_S\,[1-(1-p\,s_S)\,s_D]$, (iv) $(1-p\,s_D)\,s_S(1-p\,s_S)\,s_D$, (v) $(1-p\,s_S)\,s_D[1-(1-p\,s_D)\,s_S]$, (vi) $2(1-p\,s_D)\,s_D[1-(1-p\,s_D)\,s_D]$, (vii) $[(1-p\,s_D)\,s_D]^2$.

(ii) Now, we have adult males as well as females who will produce either two sons (F_{SS}), or a son and a daughter (F_{SD}), or two daughters (F_{DD}): $\mathbf{P}_2 = [M\ F_{SS}\ F_{SD}\ F_{DD}]^{\mathrm{T}}$. Next, offspring are produced. Parents each contribute half their genetic material to the offspring. Male reproductive success also depends on the per capita availability of females. Adults are assured survival. The second projection matrix is:

$$\mathbf{A}_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ F_{SS}/(2M) & 1/2 & 0 & 0 \\ F_{SD}/(2M) & 0 & 1/2 & 0 \\ F_{DD}/(2M) & 0 & 0 & 1/2 \\ 0 & 1 & 1 & 1 \end{bmatrix} \tag{13}$$

(iii) Now, we have adult males and females as well as the three types of broods: $\mathbf{P}_3 = [M\ SS\ SD\ DD\ F]^{\mathrm{T}}$. This is where things become interesting due to effects of juvenile mortality during the period of parental care. Sons have a baseline survival of s_S and daughters s_D. One can think of these baselines as the survival of juveniles if their sibling were artificially removed prior to hatching or birth. The survival of an individual offspring is, however, also dependent on the survival (hence sex) of its sibling. Specifically, these baseline survival rates are multiplied by either $1-p\ s_S$ if they have a brother, or $1-p\ s_D$ if they have a sister. Here, p is a penalty term between 0 and 1. If $p = 0$, offspring survival is independent of their sibling's survival. One or both offspring could die at this stage, so there are five possible brood types at the end of this stage (excluding failed broods). Together with assured adult male and female survival, this yields seven rows in our third projection matrix:

$$\mathbf{A}_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & ((1-pS_S)S_S)^2 & 0 & 0 & 0 \\ 0 & 2(1-pS_S)S_S(1-(1-pS_S)S_S) & (1-pS_D)S_S(1-(1-pS_S)S_D) & 0 & 0 \\ 0 & 0 & (1-pS_D)S_S(1-pS_S)S_D & 0 & 0 \\ 0 & 0 & (1-pS_S)S_D(1-(1-pS_D)S_S) & 2(1-pS_D)S_D(1-(1-pS_D)S_D) & 0 \\ 0 & 0 & 0 & ((1-pS_D)S_D)^2 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \tag{14}$$

(iv) Now, we have a population consisting of adults and the five possible brood compositions: $\mathbf{P}_4 = [M\ SS\ S\ SD\ D\ DD\ F]^{\mathrm{T}}$. The final process is recruitment by juveniles into the following year's mating pool and overwinter survival of adults. For simplicity, both sons and daughters recruit to the adult population with probability α. We will use this parameter to incorporate density dependence below (as in Model 1, this density dependence exists only for the juvenile stage). Adult male and female survival is s_M and s_F, respectively. Thus, the final projection matrix is:

$$\mathbf{A}_4 = \begin{bmatrix} S_M & 2\alpha & \alpha & \alpha & 0 & 0 & 0 \\ 0 & 0 & 0 & \alpha & \alpha & 2\alpha & S_F \end{bmatrix} \tag{15}$$

We set α such the population is stable over time by ensuring that the number of females in year t is equal to that in year t+1:

$$\begin{aligned} F = {} & 2\alpha F S_D^2(1-pS_D)^2(1-x)^2 + \\ & 2\alpha F S_D(1-pS_D)S_S(1-pS_S)(1-x)x + \\ & \alpha\{2FS_D(1-pS_D)[1-S_D(1-pS_D)](1-x)^2 + \\ & 2FS_D(1-pS_S)[1-(1-pS_D)S_S](1-x)] + FS_F \end{aligned} \tag{16}$$

Solving for α gives

$$\alpha = (1-S_F)/[2S_D(1-x)(1-pS_D+pS_Dx-pS_Sx)] \tag{17}$$

As with Model 1, it is sensible to only consider cases where α is less than 1 such that offspring recruitment probability never exceeds 1 (a biological impossibility). Here, this is easier to ensure than in Model 1 because adult female survival (s_F) is independent of her sex allocation decisions in this model. Thus, optimal sex allocation is less likely to cause population stability problems in this scenario, especially when adult females tend to survive to reproduce several times.

Using the same logic as in equations 5 and 6, we can solve for the stable number of males in this system:

$$M = [F(1-S_F)S_Sx]/[(1-S_M)S_D(1-x)] \tag{18}$$

As in Model 1, we can also calculate the expected number of sons and daughters that survive to independence to see how the sex ratio at independence (y) is related to the optimal sex ratio at birth. Because of the symmetry in how juvenile mortalities are penalized according to their sibling's sex and survival, this again resolves to:

$$y = (S_Sx)/[S_Sx + S_D(1-x)] \tag{19}$$

The next step is to find the equilibrium reproductive values (v) of females with different patterns of sex allocation. In particular, we are interested in female reproductive values at phase 2 (i.e. immediately after making sex allocation decisions). Here, $\mathbf{P}_2 = \mathbf{AP}_2$, where $\mathbf{A} = \mathbf{A}_1\mathbf{A}_4\mathbf{A}_3\mathbf{A}_2$. The left dominant eigenvector of this combined projection matrix $\mathbf{A}$ gives the reproductive values of individuals at phase 2. We can then calculate the fitness (w) of a mutant female using sex allocation strategy x^*:

$$w = x^{*2} v_{SS} + 2x^{*}(1 - x^{*}) v_{SD} + (1 - x^{*})^{2} v_{DD} \qquad (20)$$

The fitness of a mutant will be maximized at $\partial w/\partial x = 0$, and this will be an evolutionary stable strategy as x^{*} approaches x. Solving this gives us the optimal pattern of sex allocation:

$$x = 1/2 + \{p(S_D + S_S) - 2 + [4 - 4p(S_D + S_S) + p^2(9S_D^2 - 14S_D S_S + 9S_S^2)]^{1/2}\}/[8p(S_S - S_S)] \qquad (21)$$

Model 2: results

Although the solution appears more complex than that in our first model, the main findings are very similar: (i) selection favours mothers who produce more of the sex with greater mortality (and hence imposes a lower cost on its siblings), (ii) stronger sex allocation biases are predicted as the sexual asymmetry in mortality increases, (iii) stronger biases are predicted when the survival of one offspring has a stronger impact on the mortality of the other (i.e. high values of p) and 4) if offspring survival is independent of their siblings (i.e. $p = 0$), unbiased sex allocation is predicted (Fig. 5 left side).

There are two main differences between the results of the two models. First, the sibling competition model predicts stronger sex allocation biases than the maternal survival model, with the strongest possible biases predicted ranging from 25 to 75% sons when $p = 1$ and the difference between s_S and s_D are maximized (i.e. 0 vs. 1). Second, in the sibling competition model, the same absolute difference in son and daughter survival

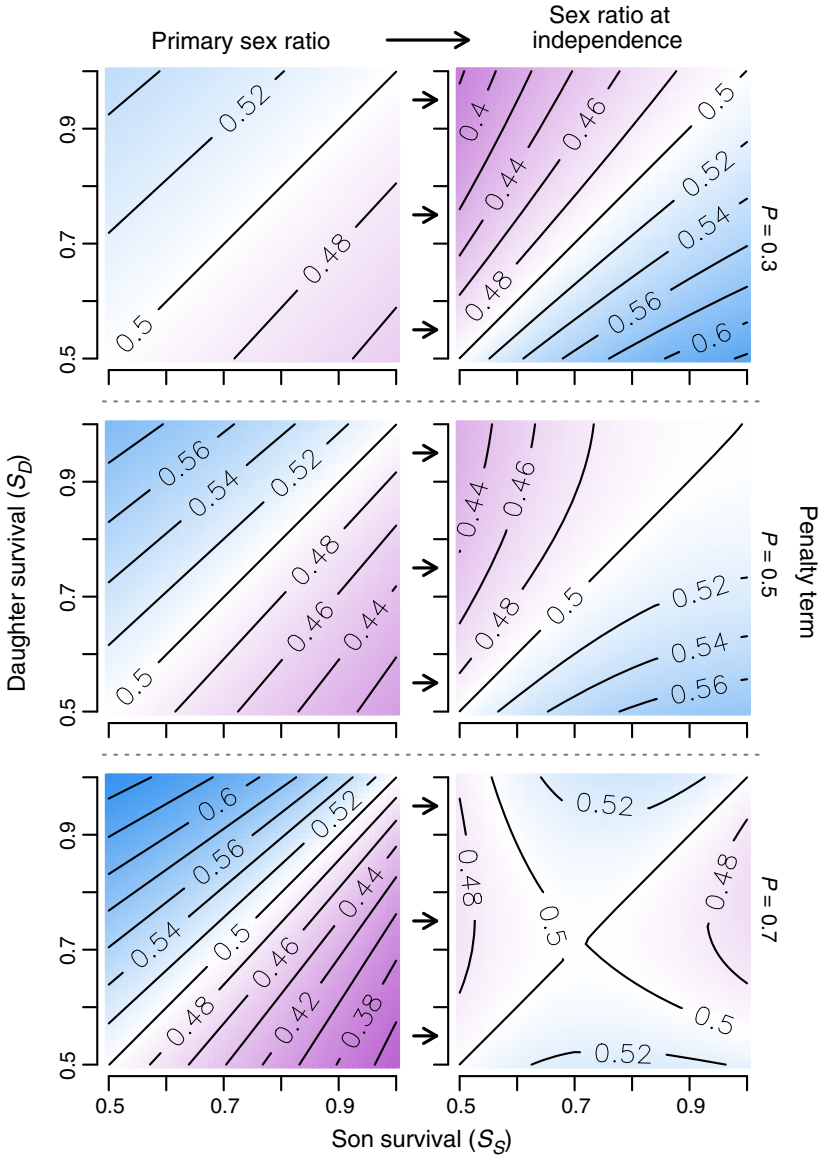

Fig. 5 Numerical examples of optimal sex allocation predictions from Model 2 (sibling competition) with respect to the survival probabilities of sons and daughters with three different levels of the penalty, p, on sibling survival. The panels on the left show optimal primary sex ratios (at fertilization), whereas those on the right show the resultant sex ratio at independence.

predicts *stronger* sex allocation biases when survival is higher (e.g. in the bottom left panel of Fig. 5, a primary sex ratio of ~0.47 is predicted when $s_D = 0.5$ and $s_M = 0.6$, but a sex ratio of ~0.45 is predicted when $s_D = 0.9$ and $s_M = 1.0$, that is the same absolute difference in offspring survival). This has implications for the relationship between the sex ratio at fertilization and independence.

Sex ratio at independence

The relationship between the primary sex ratio and the sex ratio at independence is more complex in the sibling competition model than the maternal survival model (Fig. 5 right column). In most cases, the predicted sex allocation biases are insufficient to overcome the effect of sex-specific mortality. For example, in the second example in Fig. 5, biased production of the sex with lower survival is favoured, but at independence, the sex ratio is biased towards the better surviving sex. However, exceptions to this pattern arise when there is a strong relationship between the mortality of one sibling and greater survival of the other (i.e. high values of p). The third case of Fig. 5 depicts relatively strong sex allocation biases that, in most cases, shift to a balanced sex ratio at independence. At high offspring survival values, however, the weakening of the sex ratio bias over time is not complete: some bias persists through to independence.

Discussion

We have investigated optimal sex allocation given sex-specific juvenile mortality during the period of parental care. In so doing, we have produced models that empiricists could parameterize to make quantitative predictions about optimal primary sex ratios in appropriate study systems. In general, our models support previous verbal assertions that when one sex dies more often during care, biased production of that sex is favoured (Fisher, 1930; Charnov, 1982; West, 2009). It is, however, crucial to note that this is only true if the death of an offspring prior to independence offers some kind of 'saving' (i.e. the surplus resources can be reallocated into other current/future offspring). If this is not true, then resources not used by dying juveniles are essentially wasted investment, but even if investment in one sex is more likely to represent wasted effort, unbiased sex allocation is predicted.

Past authors have suggested that juvenile mortality during parental care represents a special case of Fisher's theory that optimal sex allocation should represent equal total investment into the sexes (Fisher, 1930; Charnov, 1982; West, 2009). Our models have demonstrated that the sex allocation patterns in quite simple life-history scenarios can be surprisingly complex. The situation is not always easily captured via an equal allocation principle. That said, in our maternal survival model, with a very simple life history, the idea of equal allocation was readily implemented and correctly predicted the optimal sex allocation. We suggest that past authors were correct to discuss this scenario in terms of equal investment. This might, however, be a less fruitful way to think about the problem in more complicated, but still biologically realistic scenarios (such as our sibling competition model).

The other verbal argument that we set out to address was that when there are sex differences in juvenile mortality, any sex allocation biases would be overcome by this mortality asymmetry such that the sex ratios at fertilization and independence are negatively correlated (Charnov, 1982 p. 29; West, 2009 p. 19). In the maternal survival model, this was indeed the case. In our sibling competition model, this general pattern also emerged in scenarios that predicted relatively small sex allocation biases. However, when the survival of siblings was strongly interdependent (i.e. high values of p), strong sex allocation biases were predicted, but the sex ratio at independence was largely unbiased, and in extreme cases, the direction of the primary sex ratio bias persisted through to the end of the period of parental care. So it appears, for certain life histories at least, that the relationship between these sex ratios is complicated. It is, however, always true that a mortality bias that favours excess production of one sex will reduce the sex ratio bias at independence (interestingly, this is as far as Fisher took this idea: Fisher, 1930 p.143).

Our models predict that, all else being equal (and assuming transferrable resources), species with sex-specific juvenile mortality differences will bias sex allocation towards the sex with higher mortality. Conceptually, it is interesting to contrast this with the case of within-species variation in sex-specific juvenile mortality. For example, consider a species where son survival during care was dependent on territory quality, but daughter survival was not. This is a conditional sex allocation scenario, where one would predict mothers on high-quality territories to specialize in producing sons (because they can do so more successfully than others) and those on poor territories to produce daughters. Here, the predicted pattern within a species is opposite to that across species. It follows that experimental tests that use manipulations to induce phenotypically plastic changes in sex allocation should fail to reveal the evolved species-level response to sex-specific mortality.

In our maternal survival model, which closely resembled the original verbal argument of Fisher (1930), the sex allocation biases were not particularly strong (45–55% sons) for most of the biologically meaningful parameter space. This might explain why there are currently no published empirical studies supporting (or indeed testing) this idea in the literature (West, 2009). There are also several complicating factors that could

make detecting such a pattern challenging. For example, in sexually dimorphic species, the larger sex might suffer a higher level of mortality during parental care. On its own, this predicts overproduction of that sex. If, however, offspring of the larger sex also cost more to produce (or use resources more rapidly during care), this could cancel the survival-induced effect. Similarly, in species with highly developed parental care, sex differences in baseline juvenile mortality could be compensated for by sex-biased resource allocation during parental care rather than before (i.e. instead of biasing sex allocation). The complexities of life histories in taxa with parental care, especially birds and mammals, might mean that we never see an empirical example of the biased sex allocation envisaged by Fisher (1930). The challenge for empiricists is to identify taxa with the requisite natural history to fulfil the model's key assumptions.

In our sibling competition model, sex differences in juvenile mortality change the costs that offspring impose on their siblings. We found that, again, biased production of the sex with higher mortality was favoured, but only when there is competition among siblings (i.e. juveniles survive better when their siblings die). Similarly, Godfray (1986) demonstrated that asymmetries in the costs imposed by the sexes during juvenile competition favour excess production of the sex with a smaller competitive effect on its siblings. This idea has been neglected by empiricists (but see Sykes *et al.*, 2007), despite the fact that asymmetrical competition between the sexes occurs in several species (reviewed in Uller, 2006), including humans (Lummaa *et al.*, 2007). We suggest that this type of system could be more fruitful for empirical tests for two reasons. First, our model of sibling competition showed stronger sex allocation biases (compared to our maternal survival model), so it should be easier to detect in the wild. Second, such effects on sex allocation could occur in species with simple modes of parental care (e.g. insect species where eggs are laid in fruit/on hosts and siblings compete for a limited pool of resources), eliminating some of the confounding factors arising from parental adjustment of care in response to differences in baseline offspring survival rates.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Life-cycle graphic for our extension of model 1 to paternal survival where males provide the parental care, but females still make sex allocation decisions.
Data S1 Model 1 extension: What if mothers allocate but fathers care?

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